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| Home | Research | Services | Publications | Metinfo | Research forests | About the institute |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | Strategy | Contact |
| :--- |
| Metla » Metinfo » Forest condition » Related projects » Changes of understorey vegetation in Finland in 1985-2006 |
| Forest Condition Monitoring in Finland - National report |

Preface and contents
Monitoring programmes

Results: Crown condition
Results: Intensive monitoring

Results: related projects
Biosoil vegetation
Biosoil soil
Litter production
Soil survey design
Case Valkea-Kotinen

Publication list of the Programme

About the report


Photo: Hannu Nousiainen

## Changes of understorey vegetation in Finland in 1985-2006

By Tiina Tonteri, Maija Salemaa \& Pasi Rautio

## Summary

The understorey vegetation of 443 permanent sample plots on forested mineral-soil sites was surveyed in 1985-86, 1995 and 2006. The main causes of the observed vegetation changes were forest management practices and natural succession of the stands.

In old uncut forests, the largest changes occurred in the ground layer: bryophytes increased as lichens declined. In southern Finland, these changes are most likely due to normal forest succession, but the accumulated nitrogen deposition and long-term lack of forest fires may also have played a role. In northern Finland, reindeer grazing is the main factor in the decline of lichens. As for vascular plants, the total cover and number of species in the dwarf shrub, graminoid, and herb groups remained relatively stable. On the species level, the cover of bilberry (Vaccinium myrtillus) remained constant, but that of cowberry ( $V$. vitis-idaea) decreased on fertile and increased on less fertile sites.

In forests with regeneration cuttings, the cover and the number of species of herbs and graminoids increased soon after cutting, but the cover of dwarf shrubs declined. Within 20 years after cutting, the cover of herbs and graminoids started to decrease, but the number of species remained high. At that point in time, the cover of cowberry had nearly returned to its precutting level but the cover of bilberry still was only one fourth of that in the previous forest stage. In addition, bryophytes and lichens suffered with the regeneration cuttings; the species adapted to fertile sites suffered more than did those favouring less fertile sites.

After intermediate cuttings, cowberry and bilberry benefited from the increased amount of light. The cover of graminoids decreased, probably because they suffered from competition by dwarf shrubs.

## Background

The abundance relationships between the understorey plant species of Finnish forests have changed significantly over the last 60 years (Reinikainen et al. 2000, Mäkipää \& Heikkinen 2003). The greatest changes in vegetation took place before the 1980s. Silvicultural practices changed radically after the 1950s, which has greatly modified the environmental conditions of forest plants. As a result, the volume of the growing stock has increased, stands have become denser, and the proportion of young stands has increased (Tomppo 2000, Peltola \& Ihalainen 2012). The overstorey stand structure has a considerable influence on the understorey vegetation through shading and via
regulation of the moisture and nutrient levels. In addition, deposition of nitrogen, which experienced a peak in the 1970s-1980s, may have had some direct and indirect impacts on understorey vegetation because nitrogen is a growth-limiting factor in boreal forests. The composition of plant communities reflects the species-specific optima and tolerances with respect to nitrogen availability (Heikkinen \& Mäkipää 2010), and slightly elevated N deposition may change community structure, stimulating, for example, moss growth (Salemaa et al. 2008a).

In this paper, we report upon and analyse the large-scale changes seen in understorey vegetation at an extensive level. The same 443 permanent sample plots on mineral-soil sites were surveyed in 1985-86, 1995, and 2006
(Fig.1). We present the average values for percentage cover and number of species or species groups in two ways:

1) for different boreal subzones and soil fertility levels (i.e., site types; see Hotanen et al. 2008) and 2) by silvicultural treatment: uncut forests, forests with regeneration cuttings, and forests with intermediate cuttings.


Figure 1. Location of sample plots and subzones of the boreal boreal zone in Finland (left). The point symbols of the plots indicate site types and silvicultural treatments during different time periods (right).

## Vegetation changes in 1985-2006, over all silvicultural treatments

The understorey vegetation of 443 permanent sample plots on forested mineral-soil sites was surveyed in 1985-86, 1995, and 2006. Plot-specific sums of percentage cover and number of species were calculated in six plant groups: seedlings and saplings of trees and shrubs (height $<50 \mathrm{~cm}$ ), dwarf shrubs, graminoids, herbs, bryophytes and lichens. Mean percentage cover and mean number of species or species groups in each plant group were calculated across inventory years and three subzones of the boreal zone in Finland. The number of species was also given for different forest site types (fertility gradient). The results are presented in Fig. 2 (pdf).

## The number of herb and graminoid species has increased slightly

Increase of herbs and graminoids has taken place mainly with fertile site types (herb-rich forests and herb-rich heath forests) (Fig. 2, pdf), where these species are most abundant. Further, the cover and the number of tree and shrub species in the field layer (height: $<50 \mathrm{~cm}$ ), have increased throughout the country in all site types (Fig. 2, pdf).

## Lichens have declined throughout the country

Both the cover and the number of lichen species groups have declined nationwide (Fig. 2, pdf). The decrease in the
number of species groups has been most prominent in mesic and sub-xeric heath forests. These results are consistent with the findings of Mäkipää \& Heikkinen (2003). There were no clear temporal trends in cover or the number of species groups in bryophytes. However, the abundance relationships between bryophyte species have changed.

## Vegetation changes in 1985-2006: The effect of silvicultural treatments

Mean percentage cover and mean number of species in each plant group were calculated across inventory years and silvicultural treatments for two soil fertility levels separately. Also mean percentage cover of some selected taxa and means of stand characteristics were included. The results on percentage cover are presented in Figs. 3a-3f (see the table), and stand characteristics in Fig. 3g (pdf). The results on number of species are presented in Fig. 4 (pdf).

| Links to Figure 3a-g |  |
| :---: | :---: |
| 3a | Trees and shrubs (height < <br> 50 cm ) |
| 3b | Dwarf shrubs |
| 3c | Graminoids |
| 3d | Herbs |
| 3e | Bryophytes |
| 3f | Lichens |
| $3 g$ | Stand characteristics | uncut forests

## Old and young uncut forests

Cowberry and bilberry cover was stable in old but increased in young ,
In old ( $>55$-year-old) uncut forests, the cover and number of species have remained relatively stable within all plant groups for vascular plants (Figs. 3a-d, see the table, and Fig. 4, pdf). The cover of bilberry (Vaccinium myrtillus) has remained constant, but that of cowberry ( $V$. vitis-idaea) has slightly decreased on fertile sites (Fig. 3 b , pdf) while increasing on less fertile sites. On the other hand, the cover of both Vaccinium species has increased in young uncut forests. Cover of heather (Calluna vulgaris) shows a clear decrease on less fertile sites and a slight decrease on fertile ones. The cover of graminoids and herbs has decreased, especially in young uncut forests (Figs. 3 c and $3 \mathrm{~d}, \mathrm{pdf}$ ).

The changes in the cover of dwarf shrubs may be explained by the increase in growing stock, natural succession, low precipitation in the summers of 1995 and 2006, and between-species competition. Norway spruce dominates most fertile sites, whereas the majority of less fertile sites are dominated by Scots pine. The increased cover of tree canopies during stand succession (Fig. 3g, pdf) has decreased the amount of light and affected the species relationships in the understorey vegetation.

## Bryophytes increased while lichens declined

In uncut forests, the greatest changes have occurred in the ground layer: the cover of bryophytes has increased as the cover of lichens has decreased (Figs. 3e and 3f pdf). On less fertile sites, Pleurozium schreberi and Dicranum spp. have increased. On fertile sites, the pattern is quite different: Hylocomium splendens has expanded its cover, but the Dicranum spp. have decreased. Even the number of lichen species groups has fallen. The decline of lichens in northern Finland is largely caused by reindeer grazing.

In southern Finland, possible causes for the changes include increased shading by tree canopies, greater competition, lack of forest fires, and long-term accumulation of nitrogen originating from deposition. The increased cover of bryophytes and the decline in that of lichens could indicate some eutrophication on less fertile sites. Even in this case, the increment of growing stock and increased shading by closing canopies may have rendered the light and moisture conditions more favourable for bryophytes.

## Forests with intermediate cuttings

## Cowberry and bilberry benefited from increased light after intermediate cuttings

Intermediate cuttings (i.e., cuttings between regeneration cuttings) have increased the cover of dwarf shrubs (Fig. 3b, pdf). Both Vaccinium species have increased, but heather has decreased since the cutting. Vaccinium species are likely to benefit from the increased amount of light after thinnings, even though the volume of growing stock increases soon after the treatment. On the other hand, the cover of heather remained low for decades after the
cutting. Despite the increased amount of light, graminoids showed a declining trend after cutting (Fig. 3c, pdf). Both rough small-reed (Calamagrostis arundinacea) and wavy hair-grass (Deschampsia flexuosa) manifested this trend. They probably cannot cope with the competition from the closed mat of dwarf shrubs. No clear trends could be found for herbs after these cuttings (Fig. 3d, pdf). Seedlings and saplings of trees and shrubs $<50 \mathrm{~cm}$ increased in the first inventory after the cutting, but their cover fell slightly after that (Fig. 3a, pdf)

Bryophyte species differed in their response to intermediate cuttings
Bryophytes decreased slightly immediately after cuttings but gradually recovered later on. This pattern was typical of Pleurozium schreberi (Fig. 3e, pdf). Hylocomium splendens did not react so much to intermediate cuttings but showed an overall strong increasing trend as the forests matured. Dicranum polysetum increased after cutting on less fertile sites but showed a slight decrease on fertile ones. This species is sensitive to shading by Pleurozium and Hylocomium (Salemaa et al. 2008b). The total cover of lichens declined during the study period, regardless of the time of cutting, a trend also found in uncut and regenerated forests (Fig. 3f, pdf). The same was true for reindeer lichens (Cladina spp.).

## Forests with regeneration cuttings

Both early and late successional species persisted 20 years after regeneration cutting
The cover and number of herb and graminoid species increased after regeneration cuttings, whereas the abundance of dwarf shrubs declined (Figs. 3b, 3c, 3d and 4, pdf). Within 20 years after cutting, the cover of graminoids and herbs started to decrease as both shading by growing trees and competition with other species grew. At this stage, the number of species was larger than for mature stands, since early successional graminoids and herbs were still present.

Regeneration cutting and soil preparation dramatically changed the environmental conditions (Fig. 3g, pdf). The amount of light increased, and temperature and moisture conditions changed. Nutrients were released from both the humus layer and the logging residues. Furthermore, as trees were not competing for resources, there were more nutrient resources available for rapidly growing graminoids and herbs.

Bilberry suffered more than cowberry from drought and increased light
Twenty years after regeneration cutting, the abundance of bilberry was only one fourth of the original cover in mature stands (Fig. 3b, pdf). In the same time, the abundance of cowberry grew to reach nearly its original, precuttings level. Thick-leafed cowberry is more resistant to a larger amount of light and drought after cuttings than is the shade-tolerant, thin-leafed bilberry, and it can utilise these resources effectively in its growth. However, cuttings and soil preparation damage the rhizomes of both species, and their below-ground biomass needs decades to recover and reach the level found in mature forests.

Bryophytes and lichens' recovery after cutting took a long time
The cover of bryophytes and lichens declined after regeneration cuttings (Figs. 3e and 3f, pdf). Bryophyte species favouring fertile sites suffered on account of cuttings more than did those adapted to less fertile conditions. The shade-thriving Hylocomium splendens recovered more slowly than Pleurozium schreberi and Dicranum polysetum, which are more resistant to direct sunlight. Lichens are usually severely damaged by cuttings, and recovery from mechanical destruction and soil exposure can take decades.

## Future trends in forest vegetation

Future development of forest vegetation will depend on silvicultural practices, stand age and structure, and the proportions of tree species in the forests. Greater use of wood for bioenergy, including uprooting of stumps, and removal of logging residues are likely to cause even more vegetation changes than do the traditional regeneration cuttings. Atmospheric deposition of pollution, reindeer grazing, and control of forest fires will continue creating pressure especially for species that thrive on less fertile sites.

Climate change can affect the understorey vegetation directly by altering temperature conditions and precipitation,
but indirect influences through changes in tree stands and soil properties may be even more important.

## Methods

## Sampling and fieldwork

Understorey vegetation on 443 mineral-soil sites was surveyed in 1985-86, 1995 and 2006 (Fig. 1). These sample plots are a subset of ICP Level 1 plots as well as of a network of 3,000 permanent sample plots established in 1985-86 in association with the 8th National Forest Inventory (Reinikainen et al. 2000, Tonteri et al. 2005).

The data include both unmanaged and managed stands. On 92 of the plots, there were no cuttings in 1975-2006. In all, 72 of the plots were in old uncut forests, aged 55 years or older, and 20 plots were in uncut forests younger than 55 years. Regeneration cuttings were performed on 105 sample plots and intermediate cuttings on 246 sample plots in 1975-2006. All cuttings that took place between regeneration cuttings (usually thinnings) were included in intermediate cuttings.

Plant species were identified, and their percentage cover was estimated, for four sampling units (quadrats of size 2 $\mathrm{m}^{2}$, for $8 \mathrm{~m}^{2}$ in total on each plot), positioned in exactly the same locations on each of the three sampling occasions.

## Calculations

We calculated the plot-specific sums of percentage cover and number of species in six plant groups:

- seedlings and saplings of trees and shrubs (height $<50 \mathrm{~cm}$ )
- dwarf shrubs
- graminoids
- herbs
- bryophytes
- lichens

For the full dataset, temporal changes in percentage cover and number of species or species groups (mean $\pm \mathrm{SE}$ ) in each plant group were analysed across three subzones of the boreal zone in Finland. The number of species was also given for different forest site types (fertility gradient). In the case of bryophytes and lichens, species groups including some or all species from the same genus were used for some taxa instead of species. For instance, in genus Cladina the species were treated separately, except that C. arbuscula and C. mitis were combined to form a species group.

Furthermore, temporal vegetation changes in young and old uncut forests, forests with intermediate cuttings, and forests with regeneration cuttings on different occasions were compared. In this case, the site types were classed into two groups. The group 'fertile sites' contained site types ranging from herb-rich forests to mesic heath forests, whereas 'less fertile sites' contained sub-xeric and xeric heath forests. Temporal changes in percentage cover were calculated for plant groups as well as for some species and genera. The number of bryophyte species (not species groups) was calculated.

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Trees and shrubs (h<50 cm)




Bryophytes


Dwarf shrubs




Lichens


Graminoids


Herbs




Figure 2. Mean percentage cover and number of species ( $\pm$ standard error) in different plant groups. Percentage cover and number of species are calculated across the boreal subzones. Number of species is also given across forest site types (fertility levels).

Subzones of the boreal zones
HB-SB = Hemiboreal and Southern boreal
$\mathrm{MB}=$ Middle boreal
NB = Northern boreal
Forest site types
HRF-HRHF = herb rich forests and herb-rich heath forests
MHF $=$ mesic heath forests
SXHF = sub-xeric heath forests
XHF $=$ xeric heath forests


Figure 3a. Mean percentage cover ( $\pm$ standard error) of tree seedlings/saplings and shrubs (height $<50 \mathrm{~cm}$ ) in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting.

Silvicultural treatments
Number of plots ( n ) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 = regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 $=$ regeneration cutting in 1985-1995 $(\mathrm{n}=23$ and $\mathrm{n}=17)$
RC 75-85 $=$ regeneration cutting in 1975-1985 $(\mathrm{n}=14$ and $\mathrm{n}=13)$
IC 95-06 $=$ intermediate cutting in 1995-2006 $(\mathrm{n}=59$ and $\mathrm{n}=43)$
IC 85-95 $=$ intermediate cutting in 1985-1995 ( $\mathrm{n}=48$ and $\mathrm{n}=30$ )
IC 75-85 $=$ intermediate cutting in 1975-1985 ( $\mathrm{n}=46$ and $\mathrm{n}=20$ )
Young uncut $=$ under 55-year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=8$ and $\mathrm{n}=12$ )
Old uncut $=$ over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$.

Dwarf shrubs



Vaccinium vitis-idaea


Empetrum nigrum






Figure 3b. Mean percentage cover ( $\pm$ standard error) of dwarf shrubs and some selected taxa in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting.

## Silvicultural treatments

Number of plots (n) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 $=$ regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 $=$ regeneration cutting in 1985-1995 $(\mathrm{n}=23$ and $\mathrm{n}=17)$
RC 75-85 $=$ regeneration cutting in 1975-1985 $(\mathrm{n}=14$ and $\mathrm{n}=13)$
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Young uncut $=$ under 55-year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=8$ and $\mathrm{n}=12$ )
Old uncut $=$ over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$.

Herb-rich and mesic heath forests
Sub-xeric and xeric heath forests


Deschampsia flexuosa


Calamagrostis arundinacea


Luzula pilosa






Figure 3c. Mean percentage cover ( $\pm$ standard error) of graminoids and some selected taxa in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting.

Silvicultural treatments
Number of plots ( n ) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 $=$ regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 $=$ regeneration cutting in 1985-1995 $(\mathrm{n}=23$ and $\mathrm{n}=17)$
RC 75-85 = regeneration cutting in 1975-1985 ( $\mathrm{n}=14$ and $\mathrm{n}=13$ )
IC 95-06 $=$ intermediate cutting in 1995-2006 $(\mathrm{n}=59$ and $\mathrm{n}=43)$
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IC 75-85 = intermediate cutting in 1975-1985 ( $\mathrm{n}=46$ and $\mathrm{n}=20$ )
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Old uncut = over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$.

Herb-rich and mesic heath forests
Sub-xeric and xeric heath forests


Figure 3d. Mean percentage cover ( $\pm$ standard error) of herbs and some selected taxa in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting.

## Silvicultural treatments

Number of plots (n) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 = regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 $=$ regeneration cutting in 1985-1995 ( $\mathrm{n}=23$ and $\mathrm{n}=17$ )
RC 75-85 = regeneration cutting in 1975-1985 ( $\mathrm{n}=14$ and $\mathrm{n}=13$ )
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Young uncut $=$ under 55-year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=8$ and $\mathrm{n}=12$ )
Old uncut $=$ over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$

Herb-rich and mesic heath forests
Sub-xeric and xeric heath forests


Figure 3e. Mean percentage cover ( $\pm$ standard error) of bryophytes and some selected taxa in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting.

## Silvicultural treatments

Number of plots ( n ) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 = regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 $=$ regeneration cutting in 1985-1995 $(\mathrm{n}=23$ and $\mathrm{n}=17)$
RC 75-85 $=$ regeneration cutting in 1975-1985 $(\mathrm{n}=14$ and $\mathrm{n}=13)$
IC 95-06 $=$ intermediate cutting in 1995-2006 $(\mathrm{n}=59$ and $\mathrm{n}=43)$
IC 85-95 $=$ intermediate cutting in 1985-1995 $(\mathrm{n}=48$ and $\mathrm{n}=30)$
IC 75-85 $=$ intermediate cutting in 1975-1985 ( $\mathrm{n}=46$ and $\mathrm{n}=20$ )
Young uncut $=$ under 55-year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=8$ and $\mathrm{n}=12$ )
Old uncut = over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$.

Herb-rich and mesic heath forests
Lichens


Cladina spp.


Cladonia spp.


Sub-xeric and xeric heath forests




Figure 3f. Mean percentage cover ( $\pm$ standard error) of lichens and some selected taxa in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting.

Silvicultural treatments
Number of plots (n) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 = regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 = regeneration cutting in 1985-1995 ( $\mathrm{n}=23$ and $\mathrm{n}=17$ )
RC 75-85 $=$ regeneration cutting in 1975-1985 $(\mathrm{n}=14$ and $\mathrm{n}=13)$
IC 95-06 = intermediate cutting in 1995-2006 ( $\mathrm{n}=59$ and $\mathrm{n}=43$ )
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Old uncut $=$ over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$.

$\begin{array}{llllll}\text { RC95.06 } & \text { RC85.95 } & \text { RC75-85 } & \text { IC95.06 } & \text { IC85.95 } & \text { IC75.85 Youna uncut Old unaut }\end{array}$
RC95-06 RC85.95 RC75-85 IC95-06 IC85.95 IC75-85 Younguncut Olduncut



Proportion of deciduous trees of the volume


80 Proportion of Norway spruce of the volume


$\begin{array}{lllllll}\text { RC95-06 } & \text { RC85-95 } & \text { RC75-85 } & \text { IC95-06 } & \text { IC85-95 } & \text { IC75.85 Younauncut Oldunaut }\end{array}$
Proportion of Scots pine of the volume


${ }_{80}$ Cover of tree crowns

 Mean temperature sum of 5 yrs $\left(5^{\circ} \mathrm{C}\right.$ threshold)


Figure 3g. Mean values ( $\pm$ standard error) of stand characteristics and the effective temperature sum in herb-rich and mesic heath forests (left panel) and in sub-xeric and xeric heath forests (right panel). The arrows denote the time of forest cutting. Please notice that these results represent the included sample plots rather than Finland's forests in general. For information on Finland's forests, please see Finnish Statistical Yearbook of Forestry (Aarne \& Ylitalo 2012).

Silvicultural treatments
Number of plots ( n ) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 = regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
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Young uncut $=$ under 55-year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=8$ and $\mathrm{n}=12$ )
Old uncut $=$ over 55 -year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=48$ and $\mathrm{n}=24$ ).


Figure 4. Mean number of species ( $\pm$ standard error) in different plant groups. Arrows denote the time of forest cutting. For bryophytes, only the year 2006 is included.

Silvicultural treatments.
Number of plots ( n ) given first for herb-rich and mesic heath forests and then for sub-xeric and xeric heath forests.
RC 95-06 $=$ regeneration cutting in 1995-2006 ( $\mathrm{n}=29$ and $\mathrm{n}=9$ )
RC 85-95 $=$ regeneration cutting in 1985-1995 ( $\mathrm{n}=23$ and $\mathrm{n}=17$ )
RC 75-85 $=$ regeneration cutting in 1975-1985 ( $\mathrm{n}=14$ and $\mathrm{n}=13$ )
IC 95-06 $=$ intermediate cutting in 1995-2006 $(\mathrm{n}=59$ and $\mathrm{n}=43)$
IC 85-95 $=$ intermediate cutting in 1985-1995 $(\mathrm{n}=48$ and $\mathrm{n}=30)$
IC 75-85 = intermediate cutting in 1975-1985 ( $\mathrm{n}=46$ and $\mathrm{n}=20$ )
Young uncut $=$ under 55-year-old stands (in 1985), no cuttings in 1975-2006 ( $\mathrm{n}=8$ and $\mathrm{n}=12$ )
Old uncut $=$ over 55-year-old stands (in 1985), no cuttings in 1975-2006 $(\mathrm{n}=48$ and $\mathrm{n}=24)$.

